

STUDIES ON THE STRUCTURE OF THE MAIZE PLANT

HUGH C. CUTLER

Chicago Natural History Museum

AND MARIAN C. CUTLER

There is a basic pattern for most grasses and this pattern is repeated throughout each plant, in reproductive as well as vegetative parts. The main axis of the maize plant bears leaves and buds on opposite sides of successive nodes. This pattern extends to the branches, the tassel, and to the ear. In the maize tassel and ear the parts and even their arrangement may be modified, but the basic arrangement is still that of the stem of any grass. This can be seen easily in the lateral branches of the tassel and in ears with only four rows of grain.

All parts of the maize plant are made up of similar units. The name "phytomer" has been applied to these (see Esau, 1943, for a discussion of this as applied to the stem). A phytomer consists of an axillary bud at its lower end, a section of the stem (the internode), and is terminated by a leaf. It corresponds to Collins' (1919) *alicole*, although his original definition included only the spikelet or pair of spikelets and not the associated portion of cob or stem.

Because the maize pattern is repeated throughout the plant we can expect almost any change in one part to be repeated in homologous parts. For example, when hairs on the leaf sheath are large and numerous, there will be large and numerous hairs on the glumes of tassel and ear. Because of this repetition of plant pattern, some organs which are not strictly homologues will reflect changes in other parts. Thus, in one race of Bolivian maize, when the tassel branches and the rows of spikelets on the central spike are nearly doubled in number, the number of rows of grains on the ear and vascular strands in the stem are correspondingly increased.

The extent of variation in the grasses is greatest in the flowering parts and least in the vegetative areas of the plant. Thus the leaves are still arranged dichotomously in the Bolivian maize even though the number of tassel branches and rows of grains has been doubled.

MATERIALS

Maize.—

We studied most of the known varieties of maize in our plantings in Brazil, Bolivia, Cuba, and the United States. Some others we were able to study in the field or in dried specimens of ears. Plant-breeders and geneticists furnished material of especially interesting mutants. Two collections of this material were of great interest. One was the Central American and Mexican maize assembled by Dr. Paul C. Mangelsdorf and from which many chromosome knob positions had been determined by Dr. James Cameron. The other was a collection of inbred lines for which Dr. William L. Brown had mapped chromosome knob positions.

Teosinte.—

Some teosinte was collected in Guatemala but most of the studies were based on material grown from seed in Bolivia. For convenience we use the common name, teosinte, instead of the combination *Zea mexicana* (Shrad.) Reeves & Mangelsdorf.

Tripsacum.—

Most of the studies were made on *Tripsacum australe* Cutler & Anderson, not only because this was the one on hand when the work was under way in Brazil but because it has been reported to lack terminal knobs on the chromosomes (Graner & Addison, 1944), and is the most southern of the 18 (n)-chromosome *Tripsacum* species.

Manisuris cylindrica (Michx.) Kuntze.—

Material of this species was collected in Texas and Florida. A series of related varieties was studied in herbarium material from southeastern United States.

METHODS

Most of the studies were made on dried ears and tassels. The cobs and glumes of many varieties, especially some from North and Central America, were hard to dissect so young green ears grown in Brazil, Bolivia, Cuba, and the United States were used for these varieties. Young ears have nearly all the characters of a mature ear except color.

In cases where paraffin sections were desired, ears collected the day the silk appeared were fixed in Carnoy's fixative. At this stage most of the structures are fairly well formed, although their relative sizes are not the same as those in the mature ear. After being embedded in paraffin these ears could be cut easily and safranin- and haematoxylin-stained sections studied and compared.

Many cross- and longitudinal-sections of the stem and ears were cut free-hand and photographed by floating them onto a glass plate in the negative holder of an enlarger. The projections of these sections, made on standard enlarging paper, were studied, compared, and measured more accurately and rapidly than would be possible with the sections themselves.

When the retting methods described by Evans (1928), Sharman (1942), Reeves (1946), and Laubengayer (1946) are applied carefully, good preparations with a clearly visible network of vascular strands are obtained. We immersed some bundles in a vial of stain as directed by Evans (1928), but, since we wanted to follow more strands and had only a limited number of plants, it was more convenient to inject the stain with glass tubes which were drawn out to hypodermic needle-like points. With these we could inject several colors and trace their separate courses in the same plant. By filling the tubes one-quarter full of tap water while they were being inserted, staining of the outer rows of bundles

was avoided. Stain was added after the tube was fastened to the stem, tassel, or ear with Scotch tape. Aqueous solutions of eosin, methyl blue, and Bismarck brown were used. The tubes usually were left in place for two days although stain was carried through several nodes in a few hours.

ARRANGEMENT OF THE PHYTOMERS

If one considers the maize plant to be made of units which are moved into place like bricks in a house, then it is necessary to consider the plant as based on a spiral arrangement with each unit rotated 180 degrees. This makes the polystichous structure of the ear and the central spike of the tassel dependent only upon a change in the pattern of phyllotaxy (Weatherwax, 1935), a change which can be seen in other plants (Brieger, 1945). There have been attempts to trace this pattern in the ear and tassel. The method which shows greatest promise has been used by Mangelsdorf (1945) and takes advantage of the fact that in the distichous lateral branches of the maize tassel, and in the staminate inflorescences of teosinte and *Tripsacum*, the two rows of paired spikelets are arranged so that the pedicellate spikelet of one pair is adjacent to the similar spikelet of the other. Thus as one goes around a staminate branch of maize, teosinte, or *Tripsacum*, the spikelets are sessile, pedicellate, pedicellate, sessile. The main difficulty in applying this method is that the vertical distance between paired spikelets of the tassel is not always the same and it is necessary to measure carefully. In the ear, on the other hand, this distance is quite constant, and notations of the sessile and pedicellate spikelets can be made on squared paper. With many ears it is difficult to distinguish between pedicellate and sessile spikelets and on some ears practically impossible (Cutler, 1946). Where we have been able to apply this method to the ears, our results agree substantially with those of Mangelsdorf. There is a strong tendency to a longitudinal arrangement, a tendency made conspicuous by the vertical course of conductive tissue.

The major vascular strands run longitudinally, and although there are some connections at the nodes these are so weak that very little stain is carried to other rows of phytomers. The weakness of these connections may be seen in some maize ears with a large cob. Most of these will split longitudinally between rows of paired spikelets but resist breaking between the paired spikelets of a row, and to a lesser extent, across the rows of paired spikelets.

As an aid to the study of the relationship of the parts of the plant, we found it convenient to study the course of the vascular system. The plant may be considered to be made up of leaves, the stem to be composed of leaf traces. In the upper parts of the tassel, the number of vascular strands in the main axis is very small, and the number increases as we descend the stem and the traces of more leaves enter. Plants with many tassel branches, many nodes, and many rows on the ear usually have many vascular bundles. The number of vascular bundles in an ear appears to be larger in those ears with more grains in a longitudinal row.

An apparent contradiction to this is found in the position of ears on a single plant. Usually the highest ear has the largest number of rows of grains, and those ears borne lower on the stem, although there are more vascular bundles in the stem at the node from which these ears originate, have smaller numbers of rows of grains. In lines studied by Burdick (1947), the uppermost ears usually had eight rows of grains while the lower ears usually had four rows. Burdick attributes this to the differentiation and development of the lower ears under less favorable physiological conditions. In our observations on a large number of varieties with a wider range of row numbers, we have found Burdick's observations to be valid. Exceptions are found when a large number of ears are borne on one plant as happened on one of our crosses of Bolivian highland maize with Golden Bantam. The ear borne at the sixth node had twelve rows of grain; those at the fifth and seventh nodes had ten; at the fourth, ten; at the third and eighth nodes, eight rows. An undeveloped ear at the second node had eight rows. With the exception of plants with eight-rowed ears our notes on South American maize plantings show that the number of rows of grain on two ears from the same plant is rarely ever the same. Our notes also show that in most varieties, and again we except those which bear ears with eight rows of grains, the number of rows on the ears is greater on plants with a higher number of nodes and a higher number of vascular bundles.

There are two groups of vascular strands, the peripheral and the central or medullary. The strands pursue a nearly vertical course and these systems tend to remain distinct. When the traces from a leaf or homologous structure enter the main axis, most larger and more median bundles go almost immediately to the central region while the smaller bundles remain in the periphery and after a few nodes unite with some of the other peripheral bundles or progress to the center. The two systems are present in stem, tassel, and ear of maize, and in homologous parts of teosinte, *Tripsacum*, and *Manisuris*. The vascular system of the maize stem has been studied by Hershey and Martin (1930), Esau (1943), and Kumazawa (1940); that of the tassel by Kumazawa (1939, 1940a), and that of the ear by Reeves (1945, 1946), and by Laubengayer (1946). While there have been some studies on the relation of the stem structure to stiffness of stalk (Magee, 1948), none of the investigators has worked with a wide variety of material. There is an opportunity here for investigations of considerable practical value especially now that mechanical corn pickers are used and lodged corn stalks are more of a nuisance.

AXIS, STEM, RACHIS, COB

The axis is usually somewhat cylindrical in the stem and other distichous parts, but in a polystichous axis, like that of a many-rowed ear, the axis of each phytomer is a pie-shaped segment. Usually there is a hollow above the bud or branch. In the stem and tassel this is a longitudinal groove and in the ear a pit

or alveole. The alveole is very pronounced in teosinte, *Tripsacum*, and *Manisuris*, and its margins may partially enclose the spikelet. In some South American races of maize like "Coroico" (Cutler, 1946) and some varieties from the highlands of Peru and Bolivia and parts of Chile and Ecuador these margins or rachis flaps are inconspicuous. In other varieties, especially some of Mexico and southwestern United States, they are prominent.

For a long time we thought that prominent rachis flaps were always associated with *Tripsacum*-contaminated maize and with a high number of knobs on the chromosomes. Using chromosome knob positions determined by Dr. James Cameron for a large number of Guatemalan and South American samples of maize, and positions determined by Dr. William L. Brown for a selection of common commercial inbreds, we tried to find some correlation between the presence or absence of certain knobs and variations in the structure of the maize spikelets, both male and female. In some of the Guatemalan material there appeared to be a good correlation between prominent rachis flaps and the presence of a knob on the long arm of chromosome 3. Examination of more material showed us that not only was this incorrect, but that rachis flaps are not always correlated with high knob numbers. Some of the North American inbreds with only one chromosome knob have more prominent rachis flaps than others with seven or eight knobs.

The rachis flap resembles the auricle of the leaf in shape and this resemblance is heightened by the presence below it of the pulvinous notch, a small notch often formed at the margins of a leaf, bract, or glume, at the point of its union with the node. Like an auricle notch, it usually bears numerous hairs.

The sulci, or grooves between rows of alicoles or phytomers of the maize ear, are often deeply cut into the cob. We have found no definite geographical distribution of sulci, but they are most prominent in many-rowed ears from the Andes, Mexico, and our Southwest. In some races, as Coroico, and Altiplano from the Bolivian highlands, sulci are rarely ever present.

The vascular strands supplying the paired spikelets of the maize ear may separate nearly at once after branching out from the longitudinal vascular system but often may remain together for several millimeters. The latter is the case in some South American maize and in these varieties the paired spikelets are usually raised above the alveole. In marked contrast to this are spikelets attached so closely to the cob that they are turned toward the tip of the ear and do not lie perpendicular to the longitudinal axis of the cob.

The rachilla on which the spikelets are borne is surrounded in part by the glume. About the base of the rachilla of each spikelet of the ear is a small callus. One of the pair of spikelets is usually borne lower on the glume than the other and is surrounded by a small ring of unicellular hairs. This lower spikelet appears to correspond to the sessile one of the tassel. The rachilla of the maize spikelets is variable in thickness and in the length of its internodes. In some *Tripsacum*

and in *Manisuris* the rachilla is quite slender and the glumes, lemmas, paleas, and other parts are well separated. In teosinte and other species of *Tripsacum*, notably *T. dactyloides*, the rachilla is compacted and the parts close together. The grains of corn ears which have glumes raised above the ear and have longer and/or more slender rachillas can be pushed into the ear. The sessile ones with a compacted and short rachilla are firm. In most Guatemalan maize Andean varieties (Mangelsdorf & Cameron, 1942) could be distinguished from tripsacoid varieties by the ease with which the first could be pushed in. Ease of shattering is related not alone to the longer rachilla but to the weaker attachment of the grain to the rachilla. In segregates from crosses of Golden Bantam and Country Gentleman sweet corn many of the grains fell readily from the ear even though they were borne on compacted rachillas. This is a desirable characteristic in corn to be eaten on the cob, for the grains can be removed without the annoyance of particles of glumes and pericarp catching between the teeth. After the grain has been eaten the cob is clean and neat.

THE NUMBER OF SPIKELETS

Many of the Rottboelliae, the tribe of the Andropogoneae to which *Zea* and *Tripsacum* should belong and to which *Manisuris* does, have only one spikelet in each phytomer. In this spikelet are usually two flowers. The upper one is usually perfect and bears both pistil and stamens; the lower one is usually staminate and does not produce seeds. In cases where two spikelets are produced, one is often non-functional or staminate, while the other bears stamens and pistils. In the tassels of maize which bear seed, the sessile spikelets usually bear the seeds while the pedicellate ones remain only staminate. In teosinte and *Tripsacum* the staminate portions of the inflorescence have a pair of spikelets in each alveole, but the pistillate portion usually has only one which is functional, although a second one may occasionally develop into a functional staminate spikelet or even into a functional pistillate spikelet. Occasional clones of *Tripsacum australe* have numerous pistillate alveoles which bear pairs of spikelets. A complete series of the possible combinations in a pair of spikelets can be found in *Tripsacum*, teosinte, *Manisuris*, and maize. They are common in segregates from teosinte-maize crosses. Both spikelets may be staminate or both pistillate. When one is pistillate the other can be a pedicelled or non-functional staminate spikelet or a pedicellate and non-functional pistillate spikelet.

In maize there is nearly always a pair of functional pistillate spikelets. An exception to this was discovered by Langham (1940) in an inbred line of maize while he was making a study of single *vs.* paired pistillate spikelets in teosinte and teosinte-maize crosses. Langham concluded that the single pistillate spikelet of teosinte is governed by a single gene recessive to paired spikelets. Although he makes no mention of the tassels of his plants with single spikelets in the ear, it is probable that the tassels were not influenced by the gene he found, for Langham

was studying other tassel characters and would most likely have noticed any differences. Besides, if it is the same gene as that in teosinte, it is unlikely to have any effect on the tassel because the tassel of teosinte has paired spikelets even though these are single on the pistillate inflorescence.

Hepperly (1948) discovered an ear with single spikelets in an inbred line of corn belt dent, and has been studying this character. Hepperly told us that the tassels of his plants were different and those of the plants we have grown from seeds he supplied usually have the pedicellate spikelet of the pair reduced and non-functional but still present. There is a series of degrees of reduction of the one spikelet of the tassel, and it would be interesting to transfer Hepperly's single spikelet character to different races of maize and study any modifier complex which might be present.

Maize plants bearing teopod or corn grass genes are extremely variable in habit and in composition of inflorescences. Frequently in corn grass, and occasionally in teopod, many of the pistillate alveoles will have only one spikelet although both flowers of this may function and the spikelet will have two grains.

Illinois R4 is a corn-belt inbred line used in many combinations for the production of hybrid corn seed, but its rows of grains are usually so irregular that it is used only as the pollen parent. On many ears it is difficult to distinguish definite rows. The tassel is also more irregular than most. In R4 only one spikelet bears grains in some of the alveoles, although the other spikelet is present. The distribution of the alveoles with only one grain is occasionally so regular that the ear has an odd number of straight rows of grain over part of the ear. In spite of this we have been unable to distinguish any constant pattern for the distribution of the undeveloped spikelets.

Extra spikelets in an alveole are common in maize and are occasionally found in *Tripsacum* and *Manisuris*. Often the maize tassel will appear to bear several additional spikelets in each alveole which upon close examination may prove to be two nodes close together. This is caused by condensation of an internode (Anderson, 1944) and is distinct from multiplication (Cutler, 1946) by which additional spikelets are formed by branching within one alveole. Multiplication of spikelets within one alveole is common in the basal rows of many varieties of ears. It produces enlarged butts with irregular rows of grains. The additional spikelets are added in the same plane as the two usual ones and are forced out of line by the surrounding grains.

There are some cases of multiplication of number of spikelets in each alveole of the ear in which the additional spikelets are not borne in the same plane as the two usual spikelets but appear higher up on the ear in the same alveole. The first ears we found were among some of Dr. F. G. Brieger's crosses of pod corn with Chavantes Indian corn. These had four pairs of spikelets in some alveoles, two of them with their first glumes facing the butt and two others with their first glumes towards the tip of the ear (Cutler, 1945). The embryo of the upper grain

in the extra spikelet faced the butt just as would one which would develop in the lower flower of the usual spikelet. The extra spikelets were also found in the tassel.

Another ear with additional reversed spikelets was found in some of Dr. Mangelsdorf's collections. In this case only one spikelet was added to the usual pair but the extra one was reversed just as in Dr. Brieger's material, and the grain, even though produced from the upper flower, had the embryo on the side towards the butt. None of the alicoles on Dr. Mangelsdorf's ear had more than three spikelets and most had the usual two. We do not have a tassel from the same plant and ears grown from this seed did not have the extra spikelets.

Most studies on the structure of the ear substantiate the theory that the ear has arisen by the suppression of branches of an inflorescence. It is not surprising, then, that we occasionally find ears with more than two spikelets in each alicole. There are extremes in which the ear branches freely and looks like a greatly thickened tassel. So numerous and crowded are the branches of the tassel and ear that the plants in some variations do not produce seed. The structure of the inflorescence produced in a plant bearing the gene *ramosa*, a gene which controls one of the extreme branching types, has been described by Kempton (1921).

In most experimental fields one can find examples of flowering branches produced in the ear because they are especially common when the plant is disturbed by the presence of genes like *teopod*, *tunicate* and some of the tassel seed genes, which have radical effects, or by unnatural growing conditions, especially a change from the usual length of day to which the plant is adapted.

FLOWERS

Usually a spikelet has two glumes enclosing two flowers. The normal flower of maize, teosinte, *Tripsacum* and *Manisuris* consists of a lemma, a palea, two lodicules, three stamens, and a tricarpellate single-seeded ovary with two stigmas. In some flowers the ovary is undeveloped and in others the stamens do not develop. Functional stamens and ovary occasionally develop in the same flower, and are the rule in the upper flower of the *Manisuris* fertile spikelet.

In the Andropogoneae the upper flower usually is perfect while the lower one does not produce seeds but often bears stamens (fig. 1f). Exceptions to this are common in maize, and in one variety of sweet corn, Country Gentleman (fig. 1c), most spikelets bear two grains. The spikelets of teosinte and *Tripsacum* and *Sorghum* frequently have two grains but we have not seen this in *Manisuris*.

Even though Country Gentleman corn has been grown in many parts of the United States, two-grained spikelets are rare in other varieties of corn in North America. In South America there is no variety of maize which is characterized by two-grained spikelets, but a few spikelets with the lower flower developed are found in occasional ears of almost all varieties of highland maize.

The embryos of grains which develop in the upper flower face the tip of the ear while those which develop in the lower flower face the butt. Not all grains with their embryos on the lower side are produced in the lower flower,

and two exceptions, cases in which the alveoles had more than the usual pair of spikelets, have been mentioned. Another exception is to be found in the tips of ears of northern flint and flour corn. On a few ears we have found occasional twisted spikelets with the grains turned so the embryo faced to one side or even to the butt of the ear.

The lower flower develops later than the upper, and the grain must push into any space left between the earlier-appearing grains. Usually all the grains are so pushed out of line by this that there is no semblance of regular rows. Occasionally, however, the later lower grains are forced out to the side of the upper grains of the paired spikelets and become arranged in a straight row of small grains beside the ones from the upper flower.

The later maturation of the lower flower makes it difficult to see which ears bear the double-grained spikelet character when ears are hand-pollinated early in the season. All the fertilized grains may, if the lower ones have not yet developed silks, be borne in the upper flowers. When the ears are pollinated after the silks of the upper flowers are no longer receptive, grains are produced only in the lower flowers.

In some of Dr. Brieger's Brazilian popcorn we found ears with grains in both flowers but with the lower grain poorly developed and lacking endosperm. In appearance the extra grains resembled the structures described by Weatherwax (1925) as originating in the positions of the flower usually occupied by the stamens. These defective grains in the Brazilian popcorn did not develop in most cases unless the upper grain developed. The absence of embryo and endosperm in most of them suggested that they developed parthenocarpically but needed the stimulation of the normal grain in the same spikelet.

In our plantings of two-grained spikelet varieties in Bolivia, the character appeared to be controlled by a single recessive gene acted upon by several modifiers. In their study on Country Gentleman sweet corn, Huelsen and Gillis (1929) suggested that the two-grained spikelet character was controlled by two recessive genes. Since their classification was based on irregular *vs.* straight rows, it is possible that some ears which had a few of the lower flowers developed escaped notice because only one of the flowers in the spikelet was fertilized. A better way to classify ears for this character is to search for grains with the embryo on the butt side. It is possible that Country Gentleman corn and many of the two-grained spikelet ears from South America may bear an identical single recessive gene controlling development of the lower flowers.

There are several known genes which affect the development of the lower flower. Plants with the tunicate gene often have grains in the lower flower, sometimes even in the tassel. In plants bearing the gene for teopod, for any of the several for tassel seed, for silky, and for the "corn grass" which Dr. Singleton is studying, the lower flower usually develops.

Occasionally the stamens,, as well as the ovary, develop in the upper flower, or even in both upper and lower flowers on the ear. More commonly the tip of the ear bears purely staminate spikelets which are similar to those of the tassel.

Sometimes more than two flowers are found in the spikelets. Weatherwax (1925) has described cases in which several flowers, both pistillate and staminate, were found.

LEAVES, BRACTS, GLUMES, LEMMAS, PALEAS

That the ear of maize, and the central spike of the tassel, too, originated from the suppression of lateral branches is further suggested by the frequent occurrence of small ears in the axils of many of the husks below the main ear. Although husks or bracts are not usually found in the corn ear or tassel, one or two of the lower pairs of spikelets on an ear will occasionally be subtended by them, and the branches of the *ramosa* inflorescence mentioned earlier are often subtended by bracts. Bracts are commonly found subtending the spikelets of two peculiar mutants, teopod and corn grass.

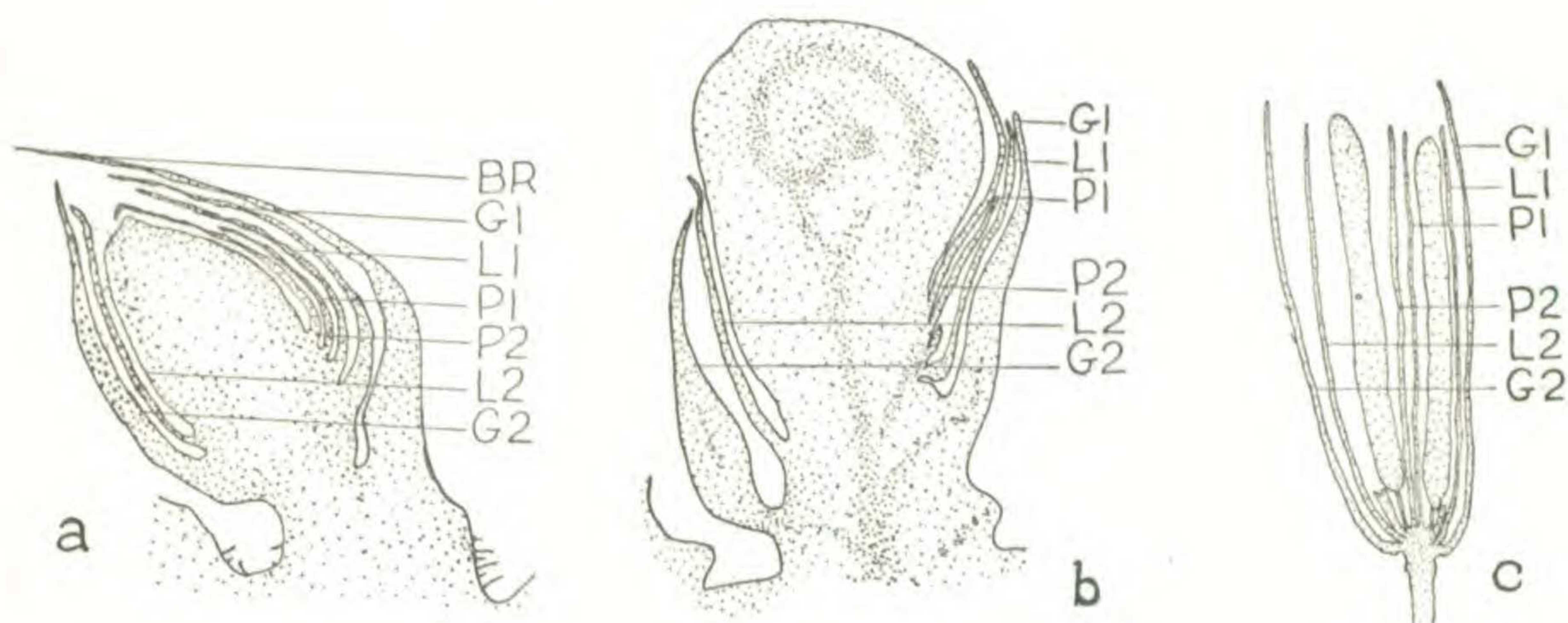


Fig. 1. Median longitudinal sections through a single spikelet of (a) teopod maize ear, (b) normal ear, (c) maize tassel.

Teopod is a dominant mutant gene on chromosome 7 which was described by Lindstrom (1925) and has been studied morphologically by Weatherwax (1929). Plants bearing this gene are extremely variable and many forms resemble teosinte in habit. On most of the plants, each pair of spikelets, in both tassel and ear, is subtended by a bract so large that it completely envelops the spikelets and the ear resembles an ear of pod corn (fig. 1a).

Corn grass is another dominant mutant, discovered by Dr. Bailey Pepper in a field of sweet corn in New Jersey. It is now being studied by Dr. W. R. Singleton and it is with his permission that we cite his first report (1947). In the few plants we grew from seed supplied by Dr. Singleton, the bract subtending the paired spikelets is only occasionally found in the tassel. Many of the lateral in-

florescences have a superficial resemblance to the inflorescence of teosinte with its many spikes each enclosed by a single husk or bract. In corn grass many of the spikelets bear both stamens and pistils.

The position of the bract can be seen in a median longitudinal section of the teopod spikelet (fig. 1a). The bract originates directly above the hump which, with its horizontal vascular system, represents the node. The bract corresponds to the leaf sheath. Occasionally the leaf blade is present, just as in the husks there may be "flags." On the glume we have seen a part equivalent to the blade of the leaf only in a few plants of teosinte and *Tripsacum laxum* in which parts of the staminate spikelet proliferate. The spikelet resembles a bulbil in the inflorescence of an agave plant and a few of them produced small roots.

There are, however, many degrees of development of the part homologous to the ligule, the fringe at the tip of most glumes. An auricle is not present in the glumes unless there is also the part equivalent to the leaf blade. The fringes along

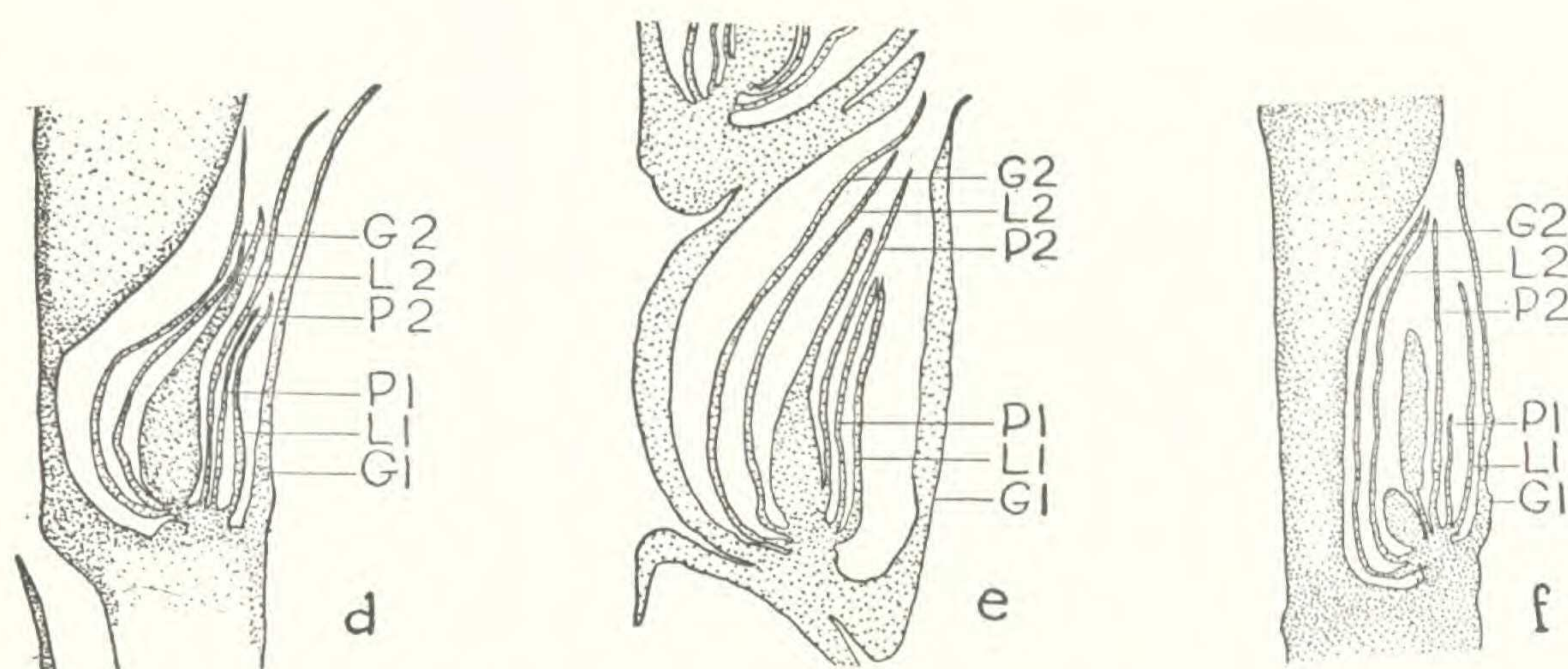


Fig. 1 (cont.). Median longitudinal sections through (d) lower or female portion of *Tripsacum* inflorescence, (e) of teosinte inflorescence, (f) inflorescence of *Manisuris cylindrica*: Br, bract; G1, lower or first glume; G2, upper glume; L1, lemma of first or lower flower; L2, lemma of second or upper flower; P1, palea of first flower; P2, palea of second flower.

the lateral margins of the glumes, lemmas, and paleas represent the margins of the leaf sheath. The keel of the bi-keeled lemma is often, but not always, the line of division between the margin of the sheath and the sheath proper. The sides of the lemma often have a vascular system, and this is lacking in the leaf-sheath margin.

At the base of the lower glume in the pistillate spikelet of the grasses we are considering is a line similar to that between the leaf sheath and the lamina of the usual maize leaf, but homologous to the junction of the leaf sheath with the node. This line is variable in width and color. It is not prominent in the staminate glumes.

We have been unable to find any color pattern of the pistillate glumes and the leaf sheaths which is associated with the glume bar or glume spot on the staminate glume, although this may be masked by other colors. This marking of deep

maroon or purple varies greatly in size, from a small dot to a patch of color covering the lower two-thirds of the maize glume. In most *Tripsacum* it is quite consistently a small spot or triangle.

The maize leaf sheath has prominent ribs marking the vascular strands. Between these one often finds hollows or pits, and there may be many hairs. These surface irregularities and hairs are found in many other grasses and recur in homologous parts of the plant. The most extreme surface irregularities are found on the lower glumes of *Manisuris*. Some of the glumes are so peculiarly sculptured that the forms have been given specific rank (*M. rugosa*, *M. corrugata*, *M. tuberculata*, and others), although it is doubtful if all of these should rightfully be considered species. The glumes of maize and *Tripsacum* are often sculptured, and while the sculpturing never reaches the extremes found in *Manisuris* and in *Hackelochloa granularis*, the irregularities are often accentuated by colored markings.

The hairs on the leaf sheaths of maize, teosinte, and *Tripsacum* are usually concentrated along the margins near the auricle. Hairs are usually inconspicuous on the female glumes but they are occasionally present in numbers proportional to those found on the leaf sheath. Some hairs are always present on the staminate glumes, and they may be abundant enough to give the glume a silky appearance. The hairs are nearly always unicellular and vary in shape from short and thick to long and slender.

The hairs which develop in the pulvinous notch, at the point of attachment of the leaf to the stem, or of the glume to the rachis, are often prominent in the maize ear. We have not been able to see material of the "corn cob fur" described by Richey (1946) and cannot be certain of the origin of the hairs in his specimen. From his photographs they appear to have a regular distribution and probably are an extreme development of the hairs on the margins of the rachis flaps, in the pulvinous notches, and those about the base of the rachilla of the spikelets. The description of the hairs, ". . . a tube with somewhat thickened walls . . ., few, if any cross walls, and they terminate in definite points, . . . extremely fragile," suggests this. It is far more likely than that they are "wild fibers from the vascular system." With the exception of some obviously fasciated forms, we have found nothing in the structure of maize for which a homologue could not be found, if not in maize, then in other grasses. All the obvious variations which distinguish tunicate, teopod, corn grass, and *ramosa* maize from the usual plants follow a definite pattern. In the case of structures described as "supernumerary silks from between the rows of grains," for example, these turned out to have a simple explanation. They were silks of partially developed lower flowers of the spikelets.

Glumes are generally smaller in South American highland maize. Not only are they smaller in the common varieties of maize, but in ears which have the tunicate character the enlarged glumes frequently do not cover the grains. This

is in contrast with North American ears which have the tunicate character, for these ears usually have glumes several times longer than the grain. The staminate glumes in South American tunicate plants often are only slightly longer than those of their normal sister plants. While some of the ears we collected might have carried the weak allele of tunicate described by Mangelsdorf (1948), small glumes were common in Dr. Brieger's crosses of pod corn and native South American corns.

While the smaller glumes in South American maize are probably due to several modifiers, there is a dominant gene, vestigial glume, which has been described by Sprague (1939). The original material was a single plant in a small planting of corn from the Belgian Congo. The glumes are greatly reduced, both in ear and tassel. Unfortunately the plant produces very little pollen because the anthers are exposed to the sun. This has made it difficult to produce a commercial sweet corn with the vestigial glume character.

Thick and hard plant parts are most prominent in plants which appear to have some tripsacoid influence, although the glumes and cobs of some Guatemalan Big Butt maize (Anderson & Cutler, 1942) and of Guarani flint from lowland South America are almost as hard as those of teosinte and some *Tripsacum*.

In ears of maize with only a few grains, all parts of the phytomers in which grains develop are hardened and have their usual colors, while the phytomers which do not develop grains are soft, flexible, and lack strong coloration.

LODICULES

Up to now we have been discussing structures which fall outside of the flower. If we consider the pattern for the monocotyledonous flower to be essentially that of the lily, the lodicules represent the remnants of the inner perianth whorl. The outer perianth whorl is absent. Usually only two lodicules are present, although Sharman (1939) has found some spikelets with three. The lodicules in maize, teosinte, *Tripsacum* and *Manisuris* are best seen shortly after the silks emerge or the day the flowers open to release the anthers. At this time the lodicules, which have swelled and thus forced the staminate flower open, are large and turgid. Even though the lodicules no longer function in the maize ear, they still become turgid at the proper time. In some of the highland Bolivian maize the lodicules were exceptionally large and had a definite vascular system.

STAMENS

Usually there are only three stamens in each staminate flower, but occasionally there are none, and sometimes two, four, or five. From their position in reference to the lodicules and to the three carpels, we know that the stamens represent only one, the outer, of two whorls of stamens of our pattern lily flower. In one specimen of maize with four anthers, the extra stamen arose between the two lateral stamens of the normal three and thus appears to represent one developed from the inner whorl of stamens. In the rather frequent staminate maize flowers with only two stamens, the remaining two were the lateral ones.

Although the stamens in the pistillate maize flowers are usually vestigial, they occasionally develop, especially when the plant is grown under peculiar conditions or is influenced by some gene with a strong effect, such as tunicate, or some tassel seed genes.

There is some variation in the diameter, length and shape of cross-section of the filament, but the most conspicuous variations in the stamen are in the anther. Colors vary widely and are related to colors in other parts of the plant. In size the anthers range from occasional minute ones (about 3 mm. long in one of our dwarf Paraguay crosses with Golden Bantam) to nearly 9 mm. (in an exceptional tassel of open-pollinated yellow dent). Most of the paired locules are cylindrical and round off suddenly at the ends but in some the ends are pointed. Although we have not seen anthers like those described as bearing the gene "warty anther" (Emerson, Beadle and Fraser, 1935), partially collapsed and partially functional anthers are common.

The pollen of maize is the largest in the grass family (Wodehouse, 1945) and is twice as large in diameter as wheat pollen. Some of our lowland Bolivian and Paraguayan plants had pollen grains which measured about 60μ , just slightly larger than the largest wheat pollen, but most maize pollen grains are about 100μ in diameter. Markings on all the grains we examined are quite uniform.

Pollen of plants with the dominant gene, gametophyte factor, fertilizes 95 to 99 per cent of the kernels of plants with the gametophyte factor when it is in competition with pollen lacking the factor. Another gene, small pollen, governs the appearance of pollen that is smaller than usual. There are numerous male-sterile genes, most of them recessive, which control shrivelled or non-exserted anthers and non-functional or abortive pollen.

PISTILS

The three carpels of the grasses under consideration are united into a unilocular, one-seeded ovule. Of the vascular strands in the midribs of the carpels, only those of the two lateral carpels, the ones which do not bear the grain, continue into the style and the two branched hairy stigmas. Occasional plants of *Tripsacum* and maize have three stigmas. In maize the style is very short and the entire silk and the bifurcate tip is stigmatic. The length and thickness of the stigmas and the number and size of hairs on them vary greatly, not only in maize, but also in teosinte, *Tripsacum* and *Manisuris*. The color of the silk in these grasses is, like that of the anthers, related to colors in other parts of the plant.

SUMMARY

1. The grass plant is made up of units called phytomers, which consist of an axillary bud at the lower end, a section of the axis, and a leaf at the upper end.
2. Although the units are modified in the various parts of the plant, their parts are homologous, whether they are in the vegetative or reproductive areas of the plant. Therefore, changes in structure of any part of a unit are often repeated

in the other units. Homologies of the parts in maize, teosinte, *Tripsacum* and *Manisuris* are discussed.

3. A study of homologous variation is of value in plant breeding because it is often possible to identify plants carrying desirable seed characters by a study of the staminate parts or the stem. Plants which will be useful in crosses can be selected at the time pollinations are made.

ACKNOWLEDGMENTS

We are indebted to the Director of the Chicago Natural History Museum for permission to publish this paper outside of the regular Museum publications. To Dr. F. G. Brieger, Escola Superior de Agricultura, Piracicaba, Brazil, we are grateful for the use of his laboratory and experimental fields while we were in southeastern Brazil, and for the opportunity to study the excellent collection of maize he has assembled and grown during his years in Brazil. Some of our material was gathered while we were working on a joint study of variation in the spikelets of native South American maize, a project which was interrupted by the war. To Dr. William L. Brown, Pioneer Hi-Bred Corn Company, Johnston, Iowa, we are indebted for growing some of our material during several seasons and for specimens of many commercial inbred lines for which he had mapped chromosome knob positions. To Dr. Paul C. Mangelsdorf, Harvard University, we are grateful for his kindness and advice while this material was being collected and studied, and for his loan of many of his collections. We want to thank Dr. Martin Cardenas, Universidad Autonoma Simon Bolivar, Cochabamba, Bolivia, for his help and the use of the University experimental fields while we were in Bolivia; and Dr. Edgar Anderson, Missouri Botanical Garden, for his stimulating suggestions and encouragement. To many others not mentioned we are indebted for the opportunity to study their material in the field and in the laboratory. Part of the South American studies was done while the senior author was a Fellow of the John Simon Guggenheim Memorial Foundation, 1942-3, 1946-7.

LITERATURE CITED

- Anderson, Edgar (1944). Homologies of the ear and tassel in *Zea Mays*. Ann. Mo. Bot. Gard. 31:325-342.
- , and H. C. Cutler (1942). Races of *Zea Mays*: I. Their recognition and classification. *Ibid.* 29:69-88.
- Bonnett, O. T. (1940). Development of the staminate and pistillate inflorescences of sweet corn. Jour. Agr. Res. 60:25-37.
- Brieger, F. G. (1945). Estudos sobre a inflorescência de milho com referência especial aos problemas filogenéticos. *Bragantia* (Brazil) 5:659-716.
- Burdick, A. B. (1947). Inheritance and morphological relations of four-kernel-row number in maize. M. S. Thesis, Iowa State College, Ames.
- Collins, G. N. (1919). Structure of the maize ear as indicated in *Zea-Euchlaena* hybrids. Jour. Agr. Res. 17:127-135.
- Cutler, H. C. (1945). Espiguetas de dois grãos no milho. *Anais Escola Sup. Agr.* (Piracicaba, Brazil) 2:423-430.
- , (1946). Races of maize in South America. Harvard Univ., Bot. Mus. Leaflet. 12:257-291.
- Emerson, R. A., G. W. Beadle, and A. C. Fraser (1935). A summary of linkage studies in maize. Cornell Agr. Exp. Sta. Mem. 180:1-83.

- Esau, Katherine (1943). Ontogeny of the vascular bundles in *Zea Mays*. *Hilgardia* 15:327-368.
- Evans, A. T. (1928). Vascularization of the node in *Zea Mays*. *Bot. Gaz.* 85:97-103.
- Graner, E. A., and G. O. Addison (1944). Meiose em *Tripsacum australe* Cutler e Anderson. *Anais Escola Sup. Agr. (Piracicaba, Brazil)* 1:213-224.
- Hepperly, I. W. (1948). Solitary spikelets in maize. Manuscript (in press).
- Hershey, H. L., and J. N. Martin (1930). Development of the vascular system of corn. *Proc. Iowa Acad. Sci.* 37:125-126.
- Huelsen, W. A., and M. C. Gillis (1929). Inheritance of kernel arrangement in sweet corn. *Ill. Agr. Exp. Sta. Bull.* 320:299-336.
- Kempton, J. H. (1921). Inheritance of ramose inflorescence in maize. *U. S. Dept. Agr. Bull.* 971:1-20.
- Kumazawa, Masao (1939). On the vascular course in the male inflorescence of *Zea Mays*. Vascular anatomy in maize. I. *Bot. Mag. (Tokyo)* 53:495-505. (English summary)
- , (1940). Further studies on the vascular course in the male inflorescence of *Zea Mays*. Vascular anatomy in maize. II. *Ibid.* 54:307-313. (English summary)
- , (1940a). On the vascular course of the leaf trace in *Zea Mays*. Vascular anatomy in maize. III. *Ibid.* 54:493-504.
- Langham, D. G. (1940). The inheritance of intergeneric differences in *Zea-Euchlaena* hybrids. *Genetics* 25:88-107.
- Laubengayer, R. A. (1946). The vascular anatomy of the mature ear and tassel of *Zea Mays*. *Amer. Jour. Bot.* 33:7a. (Abstract)
- Lindstrom, E. W. (1925). Heritable characters of maize. XXI. A new dominant hereditary character, teopod. *Jour. Hered.* 16:135-140.
- Magee, J. A. (1948). Histological structure of the stem of *Zea Mays* in relation to stiffness of stalk. *Iowa State Coll. Jour. Sci.* 22:257-268.
- Mangelsdorf, Paul C. (1945). The origin and nature of the ear of maize. *Harvard Univ., Bot. Mus. Leaf.* 12:33-75.
- , (1948). The origin and evolution of Indian Corn. *Bull. Torrey Bot. Club* 75:443-444. (Abstract)
- , and J. W. Cameron (1942). Western Guatemala, a secondary center of origin of cultivated maize varieties. *Harvard Univ., Bot. Mus. Leaf.* 10:217-252.
- , and R. G. Reeves (1939). Origin of Indian Corn and its relatives. *Texas Agr. Exp. Sta. Bull.* 574:1-315.
- Reeves, R. G. (1945). Morphology of the maize ear with reference to its origin. Manuscript.
- , (1946). Methods for studying the maize ear. *Bot. Gaz.* 107:425.
- Richey, F. D. (1946). Corn cob fur. *Jour. Hered.* 37:251-253.
- Sharman, B. C. (1939). Stamen lodicules in maize. *Nature* 144:1093.
- , (1942). Developmental anatomy of the shoot of *Zea Mays*. *Ann. Bot. n. s.* 6:245-282.
- , (1942a). Maceration method to demonstrate the vascular system in *Zea Mays*. *Bot. Gaz.* 103:627-629.
- Singleton, W. R. (1947). A second "teopod" mutation. *Maize Genetics Coop. News Letter* 21:6. (Cited by permission of author).
- Sprague, G. F. (1939). Heritable characters in maize. 50. Vestigial glume. *Jour. Hered.* 30:143-145.
- , and M. T. Jenkins (1948). The development of waxy corn for industrial use. *Iowa State Coll. Jour. Sci.* 22:205-214.
- Weatherwax, Paul (1925). Anomalies in maize and its relatives: II. Many-flowered spikelets in maize; III. Carpellody in maize. *Bull. Torrey Bot. Club* 52:87-92, 167-170.
- , (1929). Morphological nature of teopod corn. *Jour. Hered.* 20:325-330.
- , (1935). The phylogeny of *Zea Mays*. *Amer. Midl. Nat.* 16:1-71.
- Wodehouse, R. P. (1945). Hayfever plants. *Chronica Botanica Press*.